

FUNCTIONAL TRAIT DIFFERENCES BETWEEN WEEDY AND NON-WEEDY PLANTS IN SOUTHERN CALIFORNIA

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ABSTRACT

Weedy plants may have unique functional traits that distinguish them from other species. We categorized four annual plant species as weedy and five as non-weedy based on their prevalence in disturbed and invaded environments. This designation was tested in a field trial where we scattered equal numbers of viable seeds in 20 different plots and monitored density and cover over three months. The plants a priori designated as weedy had significantly greater cover and densities than species designated as non-weedy. We hypothesized that a suite of functional traits would define the weedy plant habit. We tested this hypothesis by comparing functional traits between weedy and non-weedy plant species. A principal components analysis (PCA) identified three distinct ecological clusters among the analyzed species (weedy forbs, non-weedy forbs, and grasses). The weedy habit was different from the non-weedy habit in several traits (slower growth, heavier diaspores, earlier flowering initiation, and dormant seeds requiring cold-stratification for germination). Weedy annuals in southern California appear to share a suite of traits, suggesting that their success as weeds is linked to adaptive traits. Further understanding of the traits shared among weedy plant species may help screen for native plants that are valuable for ecological restoration of highly invaded landscapes.

Key Words: California, functional trait, restoration, weedy plants.

Functional traits describe morphological, physiological, or phenological features that influence the resource acquisition and fitness of a species (Violle et al. 2007). Environmental and evolutionary forces drive the set of functional traits exhibited by a given species. Functional traits analyzed across different species can help identify plants with similar suites of traits (Gitay and Noble 1999; Violle et al. 2007). Describing functional traits is of value because, for example, it provides predictive power for how groups of species may respond to environmental change, why some species become invasive, and how species influence ecosystem function. Functional trait studies may also help identify new candidate species for ecological restoration, because the underlying causes of plant success may be trait-based (Funk et al. 2008).

We hypothesized that plants with a weedy habit would have similar suites of functional traits and that they would differ from co-occurring less weedy species. In determining which traits to sample, the ecological context of our study location was an important consideration. The southern San Joaquin Valley is widely disturbed, primarily by agricultural activities, and is an arid environment with a Mediterranean-type rainfall pattern characterized by cool moist winters and hot dry summers (Germano et al. 2011). The native upland vegetation of the region is primarily saltbush scrub habitat with abundant winter annual forbs.

The suite of analyzed traits was based on previous work and selected based on the ecological context of the study region (see Table 1 for a list of traits and predictions). Plant traits are shaped by the environment and tradeoffs. Habitat productivity and disturbance are two major environmental factors that shape plant traits (Grime 1977). In productive habitats, successful plants develop competitive traits associated with resource capture, whereas in low resource habitats stress tolerance traits predominate. In highly disturbed habitats ruderal traits dominate, such as the ability to colonize. Tradeoffs among suites of traits preclude plants from being successful in all contexts (Grime 1977; Kimball et al. 2013). For example, the traits that confer competitive ability (rapid growth and resource acquisition) are not compatible with stress tolerance traits (dense and tough tissues). We categorized traits as competitive, stress-tolerant, and ruderal in order to frame our traits within an established framework describing ecological strategies (Grime 1977). Some of our predictions about traits run counter to general patterns among weedy forbs and grasses, but make sense in the context of our study region. For instance, because of the arid environment of the southern San Joaquin Valley, we expected successful plants to be drought-tolerant and have relatively massive seeds, even though these characteristics are not usually associated with invasive weeds (however, see Funk and Vitousek 2007), which

TABLE 1. TRAITS THAT ARE MOST LIKELY RELATED TO WEEDINESS IN THE SAN JOAQUIN VALLEY. Traits are organized into the life-history strategy they most closely measure, and methods for quantifying each trait are outlined. Included are outcomes that were predicted for the weedy and non-weedy habit. Table and predictions include information from Cleland et al. 2012 (a), Cleland 2011 (b), Funk and Zachary 2010 (c), Cramer et al. 2008 (d), Funk et al. 2008 (e), Grotkopp and Rejmanek 2007 (f), Venable 2007 (g), Allen 2004 (h), Lake and Leishman 2004 (i), Seabloom et al. 2003 (j), Tyree et al. 2003 (k), Grime 2001 (l), Eriksson 2000 (m), Schutz and Rave 1999 (n), Casper and Jackson 1997 (o), Eliason and Allen 1997 (p), Philippi 1993 (q), Eissenstat 1991 (r), Poorter and Remkes 1990 (s), Venable and Brown 1988 (t), Wilson 1988 (u), Bazzas et al. 1987 (v), Grime 1984 (w), Tiffney 1984 (x), Mack and Pyke 1983 (y), Grime and Hunt 1975 (z).

Ecological strategy	Trait	Method of measurement	Literature review	Trait-specific prediction:	
				Weedy	Non-Weedy
Competitive	Growth rate	Maximum relative growth rate	Rapid growth is a competitive trait which allows plants to rapidly occupy space and deplete resources (s, w, z).	higher	lower
	Maximum biomass	Maximum total-plant biomass	Large plants are strong competitors because they have a greater demand for limiting resources (p, u, w).	higher	lower
	Above-ground competition	Specific leaf area	Greater leaf surface area exposed to sunlight allows for more competitive carbon capture and rapid growth (f, i, s, z).	higher	lower
		Leaf area ratio	Greater investment in photosynthetic tissue than in respiring tissues allows for more competitive carbon capture and rapid growth (f, i, s, z).	higher	lower
		Leaf weight ratio	Greater biomass invested in leaves than in other tissues allows for more competitive carbon capture which promotes rapid growth (f, i, s, z).	higher	lower
	Below-ground competition	Root:shoot ratio	Heavy biomass investment in roots allows more soil volume to be exploited, so that plants are more competitive for water and nutrients (c, j, o, r, z).	higher	lower
	Competitive influence	Mass of an invasive plant	Competitive species will reduce the biomass of an invasive plant (b, e, j, l, o).	lower	higher
	Germination requirements	Final percent germination (cold-stratified vs. non-stratified)	Species that germinate early (without cold-induced germination) are more competitive because they use-up space and resources before other plant seeds have germinated (a, e, g, h, n, q, y).	higher	lower
Time to germination (cold-stratified vs. non-stratified)		Species that germinate rapidly under un-stratified conditions exclude other species by growing early (a, e, g, h, n, q, y).	higher	higher	
Ruderal	Diaspore mass	Diaspore mass	Smaller diaspores may be more broadly dispersed, and their small size may enable a greater production of total diaspores per plant (d, e, j, m, t, x), but large diaspores have greater energy reserves for rapid growth (s, w, z).	larger	smaller
	Phenology	Time to flowering period initiation	Species that flower earlier can complete their lifecycle over a shorter rainfall period (h, i, v).	shorter	longer
Stress-tolerant	Drought-tolerance	Seedling drought-tolerance	Plants that can persist during periods when resources are temporarily scarce are more likely to survive and reproduce during drought (c, f, k, z).	higher	lower

TABLE 2. NINE ANNUAL PLANT SPECIES WERE COMPARED IN THIS STUDY. These species were used to identify the traits that relate to the “weedy” tendency of some native species to persist in human-disturbed and invaded San Joaquin Valley environments. Scientific names and authorities follow Baldwin et al. 2012.

Species	Family	Abbreviation	Habit
<i>Bromus madritensis</i> (L.) Husn. subsp. <i>rubens</i>	Poaceae	<i>Bm</i>	Weedy (Invasive)
<i>Ambrosia acanthicarpa</i> Hook.	Asteraceae	<i>Aa</i>	Weedy
<i>Amsinckia menziesii</i> (Lehm.) A. Nelson & J.F. Macbr.	Boraginaceae	<i>Am</i>	Weedy
<i>Heterotheca grandiflora</i> Nutt.	Asteraceae	<i>Hg</i>	Weedy
<i>Bromus carinatus</i> Hook. & Arn. var. <i>carinatus</i>	Poaceae	<i>Bc</i>	Non-weedy
<i>Clarkia unguiculata</i> Lindl.	Onagraceae	<i>Cu</i>	Non-weedy
<i>Lasthenia californica</i> Lindl.	Asteraceae	<i>Lc</i>	Non-weedy
<i>Layia platyglossa</i> (Fisch.& C.A.Mey) A. Gray	Asteraceae	<i>Lp</i>	Non-weedy
<i>Phacelia tanacetifolia</i> Benth.	Boraginaceae	<i>Pt</i>	Non-weedy

more typically avoid drought and produce numerous small seeds for wide dispersal (Table 1; Tiffney 1984; Seabloom et al. 2003).

To test our hypothesis and predictions, we selected nine species common in southern California and performed a field experiment at a decommissioned cotton field in order to determine if plants deemed weedy based on field observations were indeed more successful when starting with the same number of viable seeds in the soil. We then conducted greenhouse- and laboratory-based measurements to test for functional trait differences among five non-weedy species and four weedy species (see Table 1 for traits and predictions).

METHODS

Project Set-up and Species Selection

In the spring 2012, we identified native annual plant species within the boundaries of a former cotton field, located on the campus of California State University, Bakersfield. We found three native species and one invasive species that we classified as weedy (Table 2). Species were considered weedy if they met all four of the following criteria: 1. they occurred in disturbed areas around Bakersfield; 2. they were widespread in the United States or in California; 3. they were described in Baldwin et al. (2012) as occurring in disturbed areas; and 4. they were described as weeds in botanical literature (Whitson et al. 2001; DiTomaso and Healy 2007). We categorized three native herbaceous species and a native grass as non-weedy because they did not meet all of the aforementioned criteria (Table 2). Our designation of these species as non-weedy does not indicate that these species are never considered weedy; instead, we used this term to indicate that these species are less weedy than those we have designated as weedy. Seeds from weedy species were collected from specimens growing on campus while seeds for non-weedy species were purchased from a local southern

California native seed supplier (S&S Seeds, Carpinteria, CA).

We used both grasses and forbs for this study. The invasive grass *Bromus madritensis* L. subsp. *rubens* (L.) Husn. was included in our study as a representative of the weedy plant habit, while a native brome species, *Bromus carinatus* Hook. & Arn. var. *carinatus*, was included within the non-weedy habit. Including a grass species within each habit helped us focus on weedy plant traits while controlling for those trait differences resulting from different growth forms.

We conducted a field experiment in the winter and spring (2013) in order to verify our weedy and non-weedy habit designation. Some species may be successful in disturbed environments largely because of the abundance of their seeds in the soil. The field trial controlled for this because we seeded plots with an equal quantity of viable seeds for each species. Viability was determined from germination experiments.

In early October 2012, we prepared a field site by mowing an approximately 200 m² area of a former cotton field. We randomly identified 20 locations within the area where we cleared the first five cm of topsoil from a one m² area. In a pilot study, this depth was found to remove much of the existing soil seed bank (E. D. MacKinnon, personal observation). In each plot we added approximately 100 viable seeds for each of the nine species. A thin layer of thatch was applied to plots in the form of store-bought straw, as thatch was found in previous re-seeding efforts at the site to be necessary to prevent seeds from blowing away (E.D. MacKinnon, personal observation).

The density of individuals in plots and the canopy cover were used to quantify field success. Data were collected in late March 2013, at the peak of the growing season for most experimental species (Daubenmire 1959). Since we only sampled once, our field data did not capture field-based germination and growth dynamics. Later-growing species did not contribute a large percentage of the total canopy area at this sampling time, but they may have later in the

growing season. For these species, density of individuals was more informative than canopy cover.

We conducted a greenhouse study where we used seeds from all species to perform several experiments. We designed each experiment to evaluate a specific trait that is likely necessary for survival in disturbed and invaded environments of the southern San Joaquin Valley. For all greenhouse experiments, we used soil collected from the on-campus study plot that was sifted to remove existing seeds, and amended this soil with one-quarter part vermiculite by volume. The soil was fine grain sand and the addition of vermiculite helped keep soils from cementing in pots. A climate-controlled greenhouse was used with an automatic overhead irrigation system which kept the soil continually moist. No fertilizers were used. For all experiments, containers were randomized and reshuffled every three days to control for the effects of any greenhouse environmental heterogeneity (Grime and Hunt 1975).

Competitive Characteristics

Growth rate and maximum biomass. One hundred individuals of each species were planted into containers at a density of one individual per container (2401 inserts, Growers Solution, Cookeville, TN, USA). We knew from laboratory germination experiments that species germinated at different rates, thus to achieve similar-aged plants we staggered sowing times (Grime and Hunt 1975; Grime 2001). Seedling emergence was nevertheless sporadic, so each container was labeled with the date of seedling emergence to ensure that each sampling harvest would occur on same-aged seedlings.

The initial sample harvest occurred two weeks from the precise emergence date. We randomly selected 10 plants from each species for destructive harvest (Grime and Hunt 1975; Swanborough and Westoby 1996). For harvested plants, we removed the above-ground portion of each plant at the soil surface. To separate the roots from the soil, the entire container was submerged in water, and agitated to gently loosen the soil. Once coarse material was separated, a second rinse removed any remaining soil particles. All root material, including fine roots, was likely accounted for in this process because the fine soil particles did not adhere to the roots.

Samples were dried for 48 hr at 60°C in a drying oven (WU-05014-06 Gravity Convection Oven, Thermo Fischer Scientific, Pittsburgh, PA) before measuring dry weight for roots and shoots (CPA2P Sartorius Analytical Balance, Gettlingen, Germany). We repeated this process for 10 individuals of each species at two-week intervals for the entire study. We continued sampling for each species until it had flowered and begun to

senesce or until a loss in whole-plant biomass was found between two time periods. This loss in mass between time periods was due to senesced leaves and roots. For each sampling period, we calculated the mean relative growth rate (RGR; Hunt 1978; Grime 2001). This calculation, expressed as $\text{g g}^{-1} \text{ day}^{-1}$ or simply day^{-1} , is the change in mass over time relative to the initial plant mass, because large plants tend to grow relatively slower than small plants (Hunt 1978). To calculate the maximum relative growth rate (RGR_{max}), we used the greatest value for mean RGR obtained over the entire experiment (Dawson et al. 2011; Grime and Hunt 1975).

Allocation to leaves and roots. We harvested samples after six-weeks of growth. We chose this time period because none of the species had yet reached reproductive maturity, so they were at a more comparable stage of development (Grime 2001). For ten replicates, we measured the whole-plant leaf area (LI-3100C Leaf Area Meter, Li-Cor, Inc., Lincoln, NE), using only healthy, fully-developed leaves. After all plant material had spent 48 hr in a 60°C drying oven, we measured the dry mass of leaves, stem, and roots separately. From these measurements, we calculated the specific leaf area (leaf area divided by leaf mass [$\text{m}^2 \text{ kg}^{-1}$]), leaf area ratio (leaf area divided by the whole-plant mass [$\text{m}^2 \text{ kg}^{-1}$]), and leaf weight ratio (leaf mass divided by whole-plant mass [g g^{-1}]; Hunt 1978; Poorter and Remkes 1990).

Using the same samples harvested for leaf traits, we measured the root dry mass after roots had spent 48 hr in a 60°C drying oven. For each individual, we divided the root dry mass by the above-ground dry mass to calculate the root: shoot ratio (Grime 2001). This provided a value for the relative contribution invested in below-ground biomass.

Competitive influence on a locally abundant invader. The experimental species *Bromus madritensis* subsp. *rubens*, which was included in our weedy plant habit, is also a locally abundant invasive species. The ability of other plants to compete with this invasive grass may be key to their success. To generate a competitive interaction with this invasive grass, we grew *B. madritensis* together with another plant in 2.8L containers (product code OGTP, Growers Solution, Cookeville, TN). To ensure equal-aged seedlings for all species, we used laboratory-germinated seeds. Attaining equal-aged plants was a priority, because small initial differences in seedling size can lead to compounding competitive effects over time (Wilson 1988). We destructively harvested plants after eight weeks of growth, when all species appeared to be growing vigorously, and many were flowering. This period was chosen because the initial signs of leaf senescence were becoming visible in some species.

For biomass measurements, we could only analyze above-ground portions because entangled roots could not be distinguished between species. Using the dry biomass of *B. madritensis* shoots, we were able to quantify the relative competitive effect that each plant had on this invasive grass (Gracet 1995; Casper and Jackson 1997). This experiment also included the competitive influence that *B. madritensis* had on itself. A larger biomass of *B. madritensis* implied the competing species had little effect on the growth of the invasive grass, while a lower mass for *B. madritensis* suggested the competing species was highly competitive.

Early germination ability. We allowed seeds to imbibe in three layers of moist paper (Germination paper, Anchor Paper Company, St. Paul, MN) in sterile plastic Petri plates (Chuanren et al. 2004). We placed 20 seeds for each species, evenly divided into eight Petri plates (160 seeds total for each species) into a refrigerator at 3°C for two-months to stimulate winter conditions and cold-stratify seeds (Skordilis and Thanos 1995). As a control, eight Petri plates, each with 20 seeds, were kept in darkness in a climate controlled laboratory and were not cold-stratified.

We monitored germination every day for the first seven days and approximately every week thereafter. We considered seeds germinated when the seed coat was cracked, and part of the embryo had emerged (Shipley and Parent 1991). At the end of the 60-day stratification period, we placed both stratified and non-stratified plates together in a room temperature laboratory. Initially, we monitored germination daily to capture the spike in germination that we expected upon removing seeds from the refrigerator. We continued with approximately weekly sampling to monitor germination for 30 d.

Ruderal Characteristics

Diaspore mass. We measured the mass of the entire unit of dispersal, or diaspore (Grime and Hunt 1975; Bekker et al. 1998). The diaspore included the seed and associated dispersal aids, such as awns, pappus, and spines. We sampled and weighed a total of 160 unique diaspores for each species in order to estimate the mean mass per diaspore for each species.

Time to flowering initiation. We grew 12 plants of each species in containers (2401 inserts, Growers Solution, Cookeville, TN). Every two days, we surveyed for flowering. For most species we recorded flower-opening when petals were completely unfolded (Stenström and Molau 1992). For *B. madritensis*, flowering began when the spikelet emerged and the florets began to overlap (Baldwin et al. 2012). For *Ambrosia*

acanthicarpa Hook., we recorded flowers as open as soon as staminate heads became visible.

Stress-tolerance

Seedling drought-tolerance. For this experiment, we used laboratory-germinated seeds to ensure equal-aged seedlings for all species. For every species, we transplanted a germinated seed into one of 12, 2.8L containers (Product code OGTP, Growers Solution, Cookeville, TN) containing pre-moistened soil. After only two days of automatic overhead irrigation set to three minutes, twice per day, we moved each container to a non-irrigated portion of the greenhouse. We monitored plants daily, and randomized containers by shuffling during every visit. We recorded a seedling as dead based on curled leaves and stem, and browning of tissue (Tyree et al. 2003). After all seedlings appeared to have died, containers were irrigated for two months to confirm that all seedlings were indeed dead (Tyree et al. 2003).

Statistical Analyses

For the field experiment, we analyzed percent cover and the density of individuals. For cover data, we used an ordinal regression (JMP version 9.0.0, SAS Institute, Cary, NC), because cover data were rank ordered into one of five different percent cover categories (2.5%, 15.0%, 37.5%, 62.5%, 85.0%; Daubenmire 1959). Data for the abundance of individuals were analyzed with a generalized linear model (JMP version 9.0.0, SAS Institute, Cary, NC).

To determine the traits that were most important to the functional grouping of species, we conducted a principal components analysis (PCA; Funk et al. 2008; Diaz et al. 2004). Variables were standardized mean responses for a species derived from each experiment we performed. Since the assumptions for a PCA were not entirely satisfied, we used this analysis only for a descriptive purpose (McGarigal et al. 2000). For each component, only variables with loading scores greater than 0.3, and species positioned with sampling entity loading scores greater than 1.0 were considered to be important contributors to the principal components (McGarigal et al. 2000).

In addition to a PCA, we also analyzed each experiment individually. This is because each experiment was designed to identify a specific functional difference between weedy and non-weedy species. For the variables LWR, LAR, SLA, RGR_{max} (roots), root:shoot ratio, and competitive ability, differences among species and between habits were analyzed using ANOVA in JMP version 9.0.0 (SAS Institute, Cary, NC). Variables used in the model were habit (weedy vs. non-weedy) and species nested within habit. We

TABLE 3. RESULTS (MEAN \pm 1 SE) FROM INDIVIDUAL TRAIT ANALYSES SHOWING RELATIVE RELATIONSHIPS BETWEEN NON-WEEDY AND WEEDY PLANT HABITS. Sample size represents the number of replicates within a species. Asterisks denote significant differences between weedy and non-weedy habits (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

Variable	Units	n	Weedy	Non-weedy
Rmax (total plant)***	day ⁻¹	10	2.94 \pm 0.75	8.45 \pm 1.53
Rmax (shoot)*	day ⁻¹	10	2.24 \pm 0.55	5.10 \pm 1.02
Rmax (root)	day ⁻¹	10	4.34 \pm 1.51	9.65 \pm 3.31
Biomass	g	10	0.43 \pm 0.09	0.36 \pm 0.04
LAR	mm ² mg ⁻¹	10	7.13 \pm 1.68	5.69 \pm 0.93
LWR	g g ⁻¹	10	0.30 \pm 0.05	0.24 \pm 0.01
SLA	m ² kg ⁻¹	10	23.63 \pm 2.28	24.07 \pm 3.93
Root:shoot ratio	g g ⁻¹	10	1.68 \pm 0.43	1.66 \pm 0.12
Mass of red brome	g	7	0.56 \pm 0.10	0.49 \pm 0.09
Germination proportion***				
Stratified	%	8	58.13 \pm 7.94	76.38 \pm 7.21
Un-stratified	%	8	33.75 \pm 17.03	67.38 \pm 13.44
Time to germination				
Stratified	days	8	16.44 \pm 2.66	12.05 \pm 1.82
Un-stratified	days	8	11.91 \pm 7.44	2.84 \pm 0.90
Diaspore mass**	mg	8	3.75 \pm 2.25	2.36 \pm 1.68
Time to flowering initiation***	days	8–12	39.44 \pm 5.03	51.50 \pm 4.81
Time to seedling death	days	12	29.44 \pm 0.99	31.32 \pm 1.03

treated species as a random factor to avoid pseudoreplication. Data were transformed as necessary to meet the assumptions of parametric statistics.

For all variables that did not satisfy the assumption of normality, we used a Scheirer-Ray Hare test, which served as a non-parametric version of a two-way nested ANOVA (Sokal and Rohlf 1995; Dytham 2011) using Minitab (Release 16.0, Minitab Inc., State College, PA) and Excel (Release 2010, Microsoft Corp., Bellingham, WA). We used this test for the variables RGR_{max} (total), RGR_{max} (shoot), diaspore mass, days to flowering initiation, and drought tolerance.

For the germination experiment, we analyzed the final germination proportion, and the time to germination. These analyses allowed us to determine whether or not the requirement for cold stratification in seed germination differed between the weedy and non-weedy habits. For the final germination proportion, we used a generalized linear mixed model fit with the Leplace approximation using the R package lme4 (R foundation for statistical computing; Bates et al. 2009). The model included stratified and non-stratified (referred to as treatment), weedy and non-weedy (referred to as habit), an interaction term between treatment and habit as fixed factors and a repeated measures term as a random factor. Species were treated as random factor to correct the degrees of freedom, and avoid pseudoreplication when testing for differences between habits (Sokal and Rohlf 1995). A significant interaction term signified that the effect of the stratification treatment differed between weedy and non-weedy habits.

For time to germination, we compared days to germination initiation using a Scheirer-Ray Hare

test (Sokal and Rohlf 1995; Dytham 2011). The model included stratified and non-stratified treatments, weedy and non-weedy habits, an interaction term between treatment and habit, and species nested within habit. One species, *Amsinckia menziesii* (Lehm.) A. Nelson & J.F. Macbr., was removed from the data set because it did not germinate under non-stratified conditions. Mann Whitney tests were used to compare stratified and non-stratified treatments for each species.

RESULTS

Field-based Trial

In late March at our field plot, when most plants were fully grown, weedy species contributed greater vegetative cover than non-weedy species ($\chi^2_1 = 16.62$, $P < 0.001$). There were also more individuals of weedy species than non-weedy species ($Z = 176.23$, $P < 0.001$). This confirmed our original weedy and non-weedy habit categories.

Competitive Characteristics

Maximum growth rate and maximum total plant biomass of seedlings were assessed as traits indicative of competitive ability in the critical early growth stage. The weedy plant habit had lower maximum relative growth rates (RGR_{max}) than the non-weedy habit (Table 3). This was the case for the entire plant ($\chi^2_1 = 36.30$, $P < 0.001$) and shoots ($\chi^2_1 = 4.23$, $P = 0.039$), but not for roots ($F_{1,7} = 2.42$, $P = 0.164$). Weedy and non-weedy habits were also not different in maximum biomass attained ($F_{1,7} = 0.51$, $P = 0.499$).

Resource allocation to shoots and leaves is an important determinant of growth rates and competitive ability for light capture, while a larger resource allocation to root biomass may allow plants to become stronger competitors for water and soil nutrients. Weedy and non-weedy habits did not differ in their leaf weight ratio (LWR; $F_{1,7} = 1.07$, $P = 0.335$), leaf area ratio (LAR; $F_{1,7} = 0.63$, $P = 0.452$), or specific leaf area (SLA; $F_{1,7} = 0.01$, $P = 0.932$). Weedy and non-weedy habits were also not different in their relative biomass contribution to roots, as shown by their root:shoot ratio ($F_{1,7} = 0.01$, $P = 0.964$).

The ability to compete for space and resources was quantified in terms of the effect each species had on *Bromus madritensis* subsp. *rubens* biomass when grown in the same container. There was no difference between weedy and non-weedy habits in their competitive effect on the invasive grass ($F_{1,7} = 0.29$, $P = 0.603$). Most species resulted in *B. madritensis* biomass that was similar to that attained by *B. madritensis* plants grown under intraspecific competition. Intraspecific competition should be strong due to similar functional traits between conspecific individuals, thus most species were strong competitors.

The lack of seed dormancy allows early germination and growth, and may confer a competitive advantage. A cold-stratification treatment increased the proportion of germinated seeds to a greater degree for the weedy habit than the non-weedy habit ($Z = -3.559$, $P < 0.001$ for interaction of treatment and habit). This indicates that the weedy habit is more specifically cued to germinate under cool and moist conditions, while the non-weedy habit does not exhibit such seed dormancy. These weedy species germinated during, not after the cold stratification period, implying they are cued to germinate at the beginning of winter, when weather conditions are appropriate for growth. Although weedy species benefited from cold-stratification more than non-weedy species, contrasts showed that both habits benefited from cold stratification.

Despite greater overall germination percentage under cool temperatures, this treatment tended to slow the germination of most species. Cold-treated seeds took longer to begin germinating than seeds in the non-stratified treatment ($\chi^2_1 = 0.99$, $P < 0.001$). This effect was not significantly different between weedy and non-weedy habits ($\chi^2_1 = 0.93$, $P = 0.074$).

Ruderal Characteristics

The ability of species to disperse, a key ruderal trait, was assessed by examining diaspore mass. The weedy habit exhibited heavier diaspores than the non-weedy habit ($\chi^2_1 = 10.21$, $P = 0.001$). Because of their mass, diaspores of these species are unlikely to disperse long distances; however, they may

contain greater energy reserves that increase their chances of establishment within an existing community and their ability to compete successfully.

Early flowering, a trait that allows ruderal plants to take advantage of short resource pulses, was analyzed by counting the number of days to flowering initiation. Only six species flowered, which allowed a comparison of flowering period initiation among three weedy and three non-weedy species. Among these six, the weedy habit flowered earlier than the non-weedy habit ($\chi^2_1 = 9.45$, $P = 0.002$).

Stress-tolerant Characteristics

Drought-tolerance, which may help seedlings persist between unpredictable rainfall events, was assessed as the number of days to drought-induced seedling mortality. There was little variation among species in seedling drought-tolerance. There was no difference between weedy and non-weedy habits ($\chi^2_1 = 3.16$, $P = 0.075$).

Principal Components Analysis

Data were summarized and relationships among traits were assessed using a principal components analysis (Fig. 1). These results can be compared to a summary of the results from individual trait analyses (Table 3). With respect to the variables analyzed, the principal components analysis showed that species clustered into distinct groups (Fig. 1a). All species except *Layia platyglossa* (Fisch. & C.A. Mey.) A. Gray, *Phacelia tanacetifolia* Benth., and *Amsinckia menziesii* (Lehm.) A. Nelson & J.F. Macbr. loaded strongly on the first component; and all species except *B. carinatus* loaded strongly on the second component. The invasive grass *B. madritensis* and the native grass *B. carinatus* formed a group that was separate from forb species. The grasses were characterized by high root allocation, high total plant biomass, low growth rate, and heavy diaspores. Most non-weedy herbaceous species loaded toward relatively rapid growth, smaller total plant biomass, diaspore size, and root:shoot ratio on the first component. On the second component, non-weedy species were characterized by greater drought-tolerance and low leaf investment per plant biomass (Fig. 1a). Weedy native forbs occupied a range of plant sizes, root:shoot ratios, diaspore mass, and growth rates (first component), but all of them clustered towards higher leaf investment and relative drought intolerance (second component). One non-weedy outlier, *P. tanacetifolia*, did not load strongly on either component.

The principal components analysis also revealed relationships among traits (Fig. 1b). On the first component, diaspore mass, total plant biomass, and root:shoot ratio correlated negatively to rapid growth rates. On the second component, a tradeoff

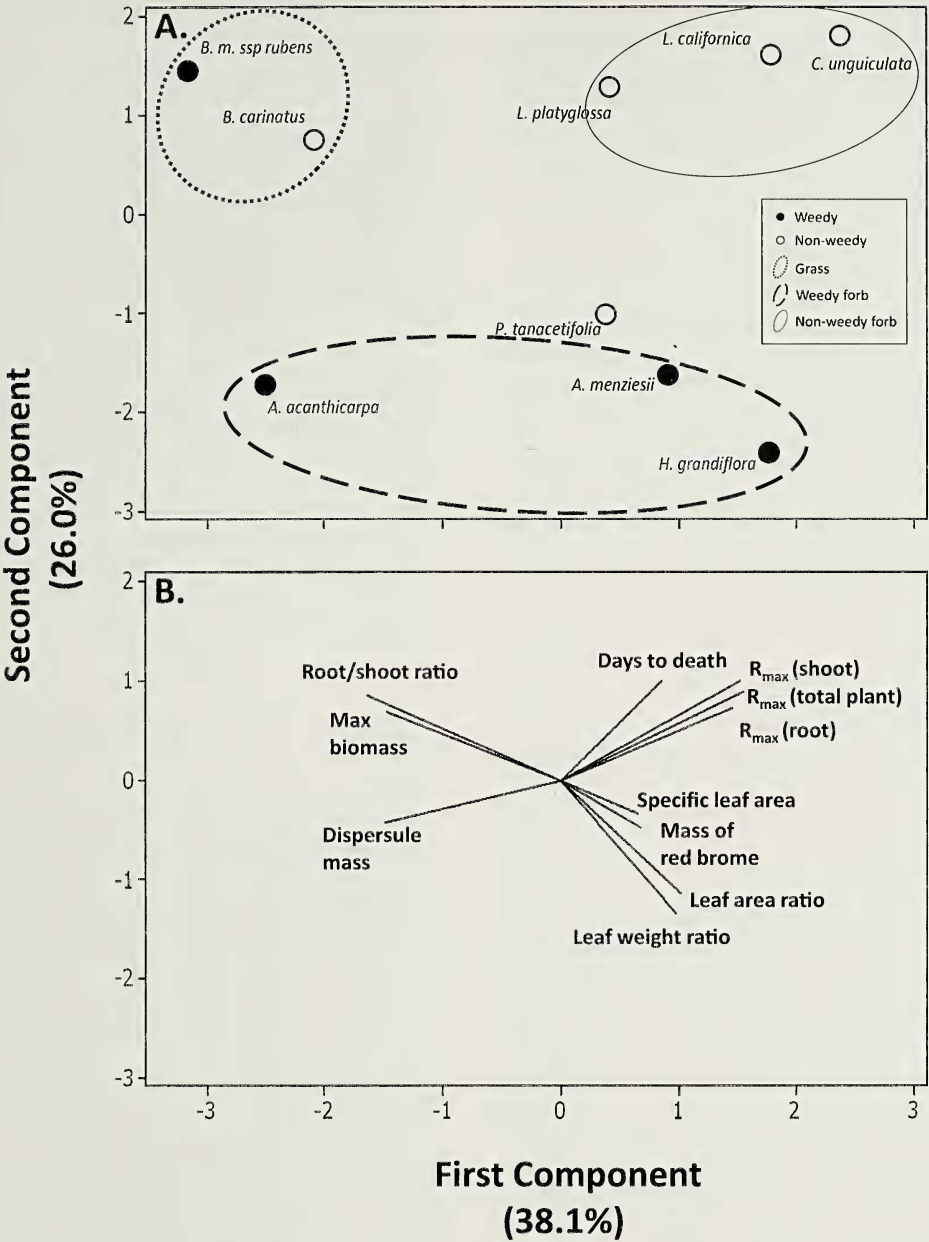


FIG. 1. Principal components analysis (PCA) completed from the mean species values for each of the variables analyzed. Species (A) and trait (B) vectors are shown as separate panels. The variables flowering phenology and cold-stratification requirement were excluded from this analysis because the data structure was not appropriate for a PCA. Ellipses show functionally similar species' cluster with respect to the variables analyzed. Each point in panel A represents a species. Species abbreviations are given in Table 2.

was observed with leaf investment traits negatively associated with root allocation.

DISCUSSION

Percent Cover and Density of Individuals under Field-conditions

Our weedy and non-weedy habit designation was confirmed by a field experiment, where we

found weedy species were more abundant than non-weedy species. Plant abundance was not confounded by seed quantity because we used the same number of viable seeds for each species in an area where the existing seed bank had been eliminated, and observations were limited to one growing season. Our results suggest that the success of these weedy species is not solely determined by seed abundance, and may be attributed to other factors (Seabloom et al.

2003; Lockwood et al. 2005). We hypothesized that functional trait differences were an important cause of these differences in abundance. Other explanations exist as well, such as differential herbivory, where the seeds of non-weedy plants were preferentially removed by seed predators, but this was not apparent based on our field observations.

Weedy and Non-weedy Species

We found that plants fell into three groups: 1. grasses, 2. weedy forbs, and 3. non-weedy forbs, with a distinction between weedy and non-weedy habits evident among the forbs (Fig. 1). The weedy forb group differed from non-weedy forbs mainly by their comparatively high leaf area investment. The grass group was characterized by relatively large total plant biomass, large root: shoot ratio, and large diaspores. Individual trait analyses demonstrated that weedy species, when compared to non-weedy species, had slower growth rate, heavier diaspores, earlier flowering period initiation, and a greater cold-stratification requirement for germination (Table 3).

The traits that were shared by weedy species are likely linked to the environmental conditions associated with the southern San Joaquin Valley. The slower growth rates found in weedy forbs suggests they are at a competitive disadvantage in terms of a lack of a capacity for rapid use of space and resources (Poorter et al. 1990; Grime and Hunt 1975; Eliason and Allen 1997; Dawson et al. 2011). However in San Joaquin Valley habitats competitive ability in terms of rapid growth may not be as important as other factors, and could even be detrimental, causing plants to deplete limited resources faster than they are replenished (Grime and Hunt 1975). The lack of a difference between weedy and non-weedy habits in seedling drought-tolerance suggests that despite arid conditions of the southern San Joaquin Valley, seedling drought-tolerance is unlikely to be an important feature differentiating weedy from non-weedy annual plants, which may instead share the tendency to avoid drought by growing only when resources are plentiful.

The ability of weedy species to initiate flowering earlier than non-weedy species may enable these plants to reproduce quickly, even during a short rainy season (Cramer et al. 2008; Eriksson 2000; Lake and Leishman 2004; Grotkopp and Rejmánek 2007). Based on the heavy diaspores of weedy species, long-distance dispersal ability does not appear to be a key factor in their ability to colonize disturbed areas (Eriksson 2000; Venable and Brown 1988; Tiffney 1984; Drenovsky 2012). However, these heavy diaspores could still be well dispersed if they have specialized structures that allow them to be dispersed by wide ranging

animals, and this appears to be the case for some species included in this study.

Although seeds of weedy species had greater germination proportion in the cold-stratified treatment, they tended to germinate at cool temperatures, rather than after the cold period had ended. Thus, instead of being cued to germinate with warming spring conditions, which is usually the case in cooler climates, these plants are instead cued to germinate at the start of winter (Keeley and Davis 2007). This is consistent with the occurrence of these plants in a Mediterranean-type climate, where cool temperatures usually coincide with adequate moisture for growth. This winter germination ability, combined with slow growth rates, could relate to a weedy strategy that enables weedy species to slowly occupy space and resources during cool winter months. This way, weedy species may be well established by the time spring arrives and other species begin to germinate. It would be valuable to compare field-based germination and coverage to test this hypothesis.

CONCLUSIONS

Based on an analysis of nine co-occurring species of the southern San Joaquin Valley of California, there appears to be a weedy suite of traits that describes the success of some annual plant species. Weedy species were characterized by several traits: slower growth, heavier diaspores, earlier flowering period initiation, and a germination mechanism cued to the cool and moist winters associated with Mediterranean-type climates. The distinctions we found between weedy and non-weedy plants may be used to locate native species from databases that could be useful for restoration (e.g., the TRY database; Kattge et al. 2011). Using native plants that resemble invasive plants functionally may be useful for exposing invasive species to competition, whereas species that differ in functional traits may be selected because they are functionally complementary to a particular invader (Funk et al. 2008). Functionally weedy native plants in particular could lead to increased native plant cover and diversity in ecosystems that, due to continuing disturbance, no longer support historic vegetation. It is possible that this form of restoration would eventually improve ecological conditions for more ambitious restoration objectives.

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